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AMIA (=KINDLEIA) FRAGOSA  
(JORDAN), A CRETACEOUS AMIID FISH, WITH NOTES  
ON RELATED EUROPEAN FORMS<sup>1</sup>

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**ABSTRACT.** Numerous well-preserved disarticulated specimens from the late Cretaceous Hell Creek Formation of Montana show that *Kindleia fragosa* Jordan, a late Cretaceous and Paleocene amiid from North America, is referable to the Recent genus *Amia*. *A. fragosa* resembles the middle Eocene *A. gurleyi* from North America, the late Paleocene *A. russelli* from France, the middle Eocene *A. kehreri* from Germany, and the Oligocene *A. munieri* from France in a number of minor but consistent skull features. *A. kehreri* and *A. gurleyi* are relatively shorter-bodied forms than *A. calva*; the two other species were probably also short-bodied, but are known only from disarticulated or incomplete material. Most differences from *A. calva* shown by the fossil forms are minor and probably primitive. These morphological differences, and close relationship of Cretaceous seas of the western interior to the Mississippi River drainage of today, indicate that *A. fragosa* is not far from the ancestry of *A. calva*.

## INTRODUCTION

Jordan (1927, p. 145) described a fossil fish from the Edmonton Formation (late Cretaceous, Alberta) as *Kindleia fragosa*, referring it to the Cichlidae. Estes (1964) demonstrated that it was an amiid, utilizing extensive material from the Lance Formation of Wyoming, and synonymized *Styliomyleodon lacus* Russell (1928) on the basis of specimens including the type bones of both described species. Russell (1968) has apparently not accepted this conclusion. Recently, Janot (1966, 1967) has described new European amiid material and has suggested that features shown

<sup>1</sup> Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 5.

by Lance Formation amiids indicate no more than specific distinction from *Amia*. We agree with this conclusion, which is documented below with some necessary qualifications, and *Kindleia* is here included in the synonymy of *Amia*.

Recent collections from the Hell Creek Formation of Montana (Sloan and Van Valen, 1965) have produced more material of *Amia fragosa*. This study is based on a Museum of Comparative Zoology collection made in 1964 by A.D. Lewis and party, from Bug Creek Anthills, west half of section 9, T 22 N, R 43 E, McCone County, Montana. Supplementary material from the same locality was provided by Dr. Robert Sloan (University of Minnesota). An American Museum of Natural History collection from the Lance Formation (localities V5711 and V5620: Estes, 1964; Clemens, 1963) was also utilized in this study. Almost all skeletal elements have been recovered in large numbers (except scales, in contrast with the Lance Formation collection). At least 94 individuals are represented in the MCZ Bug Creek Anthills sample.

Estes (1964) studied this species in detail, and we therefore discuss Bug Creek specimens only as they modify conclusions reached by that study. Order of discussion of bones follows that of Estes.

#### ORDER AMIIFORMES

##### Family Amiidae

##### *Amia fragosa* (Jordan, 1927)

*Kindleia fragosa* Jordan, 1927, p. 125

*Styliomyleodon lacus* Russell, 1928, p. 105

**Basioccipital.** Estes (1964) noted that Lance Formation basioccipitals had only one fused vertebra rather than two as in *Amia calva*. Twenty basioccipitals occur in the Bug Creek sample; nine with one fused vertebra as in the six Lance Formation specimens, and eleven with two fused vertebrae as in our six specimens of Recent *A. calva* (Fig. 2). There is a weak tendency for fusion of vertebrae to be correlated with increasing size in the Bug Creek sample; since all of our *A. calva* are approximately the same size, it is possible that such a variation exists in the Recent species as well. However, Janot (1967) has shown that variation in this feature occurs in her fossil material and suggests that it is independent of size-age variation, since even large bones may lack the additional vertebra (*ibid.*, pl. 12, fig. 2). Whatever the case, we believe that the lack of a second fused vertebra in the six Lance

Formation specimens was a chance aggregation without taxonomic significance.

The relatively short basioccipital and limited extent of the posterior brain chamber impression on it were noted for *Amia fragosa* by Estes (1964, p. 29). These features are also visible on the basioccipital figured by Janot (1967, pl. 12, fig. 6a), and differ from the widely-open brain chamber impression and somewhat longer basioccipital of *A. calva*.

*Pterotic.* Estes (1964) stated that a parietal lappet on the pterotic distinguished this species from *A. calva*. However, it is present in some of our *A. calva*, and the condition is also variable in the Cretaceous species. Pterotics of *A. fragosa* are consistently shorter than those of *A. calva*, and have a relatively greater antero-medial excavation for the frontal, reflecting the greater posterior extent of the latter noted below.

*Parietal.* The parietals lack an opening for the sensory canal. As Janot (1967) notes, this is different from the situation in *A. calva* and is a specialization of *A. fragosa*. The parietal is approximately square, rather than elongated anteriorly as in *A. calva*.

*Frontal.* Estes (1964) noted that orbital excavation in Lance Formation frontals was greater than in *A. calva*, and by comparison with *Sinamia* suggested the presence of supraorbitals for *A. fragosa*. Articulated specimens of *A. kehreri* (to be discussed below) from the Eocene of Europe indicate that supraorbitals are lacking in that related species, and they were probably also absent in *A. fragosa*. However, the late Cretaceous amiid *Enneles* does have supraorbitals (Silva Santos, 1960). The frontals appear to be relatively longer in *A. fragosa* than in *A. calva*, an estimated 2.8 times the length of the parietals, as opposed to 2.4 for the Recent species. This was determined in our disarticulated material by matching parts of bones of similar widths and general proportions, and by comparison with the related *A. kehreri*. The relatively long frontal and short parietal proportion is a primitive character, as judged by its presence in some other Mesozoic amioids (e.g. *Enneles*, *Megalurus*).

*Dermosphenotic.* This bone was not identified in the Lance Formation sample. Three specimens in the Bug Creek material resemble those of *A. calva* but are less elongated anteriorly, reflecting the relatively larger orbit of *A. fragosa*.

*Nasal.* Estes (1964) noted no difference of nasals from *A. calva*. Well-preserved Lance Formation specimens and the Bug Creek specimens all indicate a slight bifurcation of the nasal around the anterior nostril absent in our specimens of *A. calva* (Fig. 1).

*Premaxilla.* In 13 complete premaxillae, tooth count ranges from 6-9 teeth [frequency 6(1), 7(2), 8(9), 9(1)], as in *A. calva*.

*Vomer.* Number of vomerine teeth was cited by Estes (1964, p. 32) as greater than in *A. calva*. Counts based on Lance Formation and Hell Creek Formation specimens indicate a range of 18 to 24 teeth per vomer; range for the Recent species is from at

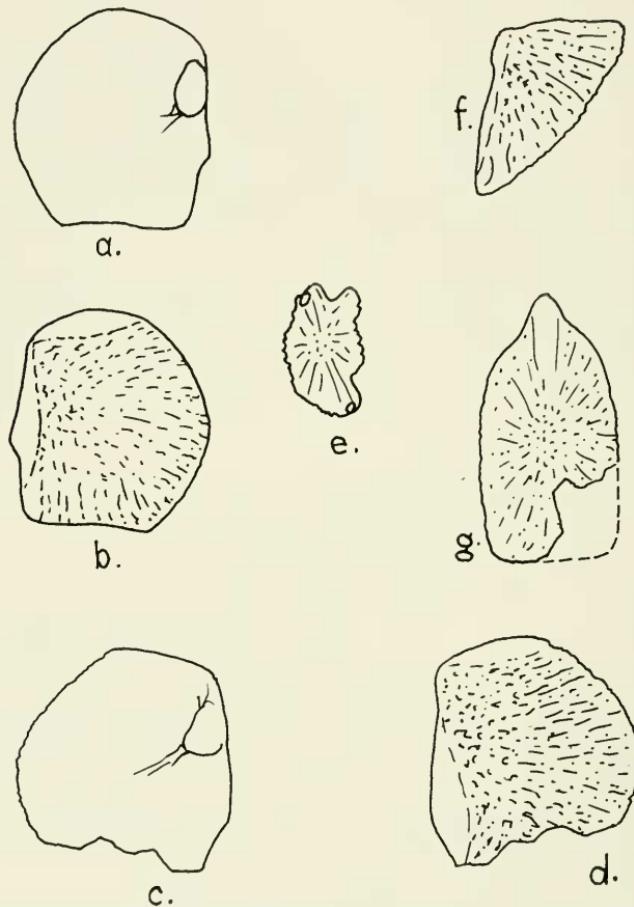


Fig. 1. *Amia fragosa*: a, medial, and b, lateral views of MCZ 9291, left operculum, unworn, unbroken; c, medial, and d, lateral views of AMNH 9315, left operculum, broken ventrally; e, dorsal view of right nasal, MCZ 9288; f, lateral view of MCZ 9293, left interoperculum; g, ventral view of MCZ 9286, gular; all  $\times 1$ . AMNH 9315 from Lance Formation, Wyoming; all others from Bug Creek Anthills, Hell Creek Formation, Montana.

least 15 to 27, bracketing the fossil count. Increased vomerine tooth count must thus be removed from the diagnosis of *A. fragosa*, but the vomerine tooth patch in *A. fragosa* always extends farther posteriorly than in the Recent species, as already indicated by Estes (1964, fig. 17a, and Fig. 3b, this paper).

**Dentary.** As in *A. calva*, the alveolar border makes a right angle with the external face of the bone (Janot, 1967, p. 146). Few dentaries are complete enough to allow tooth count, but two have 14 and one 16 alveoli, about as in our *A. calva* sample. As in *A. russelli* Janot, coronoid attachment area is deep anteriorly in relation to depth of the jaw, and depth of jaw is greater proportionally than in *A. calva*.

**Gular.** This bone was not recovered in the Lance Formation material, but two gulars have been identified in the Bug Creek collection. This is a variable bone in *A. calva*, but that of *A. fragosa* is consistently shorter and less concave when compared with bones of the same width in the Recent species (Fig. 1).

**Operculum.** The few fragmentary opercula from the Lance sample were broken and abraded posteriorly, resulting in an inaccurate restoration by Estes (1964). The Princeton specimen thought by him to confirm the rectangular restoration given (*ibid.*, fig. 16e) is Eocene rather than Paleocene as noted (*ibid.*, p. 33), and is also broken, as more recent preparation has shown. Well-preserved Bug Creek specimens show symmetrically-rounded posterior borders with an obtuse point, similar to that of the Eocene *Amia* ("*Paramiatus*") *gurleyi* (Romer and Fryxell, 1928). *A. kehreri*, and *A. russelli*. Well-preserved Hell Creek Formation and Lance Formation specimens also confirm this shape (Fig. 1). *A. calva* usually has the blunt point in a more ventral position; the ventroposterior border of the bone in the Recent form is thus relatively more elongated. Compared with height, length of operculum is less than in *A. calva* (Fig. 3).

**Suboperculum.** For bones of the same anterior height, length is somewhat less than in *A. calva* (Fig. 2).

**Interoperculum.** The same as for suboperculum (Fig. 1).

**Supracleithrum.** This bone was not identified in the Lance Formation sample. A single specimen from the Bug Creek collection is more robust than that of *A. calva* and has an external surface sculptured like that of the cleithrum (as described by Janot, 1967, pl. V, fig. 4a for *A. russelli*).

**Comments.** The large Bug Creek sample and the American Museum of Natural History Lance Formation sample thus confirm the suggestion of Janot (1967) that *Kindleia* is a junior

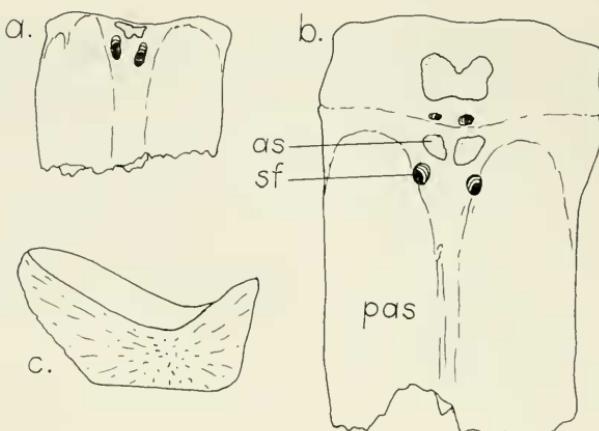


Fig. 2. *Amia fragosa*, late Cretaceous, Bug Creek Anthills, Hell Creek Formation, Montana: *a*, ventral view of MCZ 9290, basioccipital with one fused vertebra; *b*, ventral view of MCZ 9289, basioccipital with two fused vertebrae; *c*, lateral view of MCZ 9292, right suboperculum. Abbreviations: *as* = aortal supports, *pas* = parasphenoid articulation surfaces; *sf* = foramina for spinal arteries; all  $\times 3$ .

synonym of *Amia*. Operculum shape, vomerine tooth count, and fusion of vertebrae to the basioccipital resemble conditions in Recent *Amia calva* more than was indicated by Lance Formation specimens studied by Estes (1964). However, these and other features indicate specific difference from *A. calva*. A revised species diagnosis is as follows:

1. Amiids with an estimated range of body length about the same as in Recent *A. calva*, as indicated by comparison of disarticulated elements with those of the Recent species.
2. Dermal bones about 1.5 times as thick as in *A. calva*.
3. Frontals about 2.8 times length of parietals.
4. Relatively large postorbitals, probably filling cheek region; lower postorbital much larger than upper postorbital; vertical pit line present on lower postorbital.
5. Marginal teeth simple, pointed cones, palatal teeth usually stout, styliform crushers.
6. Operculum with bluntly-pointed posterior border; opercular series relatively short anteroposteriorly.
7. Supraorbital sensory canal not entering parietal.

*Related forms.* Janot (1967) has agreed with Estes (1964, p. 41) that *A. munieri* of the Oligocene of France is closely related

to *A. fragosa*. Another related form is *A. kehreri* from the middle Eocene of Germany. Complete articulated specimens of this species are in the British Museum (Natural History), collected by Walter Kühne (BMNH P33480, P33488, Messel bei Darmstadt), and in the Museum für Mitteldeutsche Erdgeschichte, Halle (Saale), collected by Dr. Horst Matthes in the Geiseltal deposits (fig. 4; pl. 1). These specimens conform to the species diagnosis given above for *A. fragosa*, although the apparent absence of the supraorbital canal in the parietal cannot be confirmed without disarticulated material. In addition, they have only about 50-55 vertebral segments (counting diplospondyl centra as one pair per segment). This low number of vertebrae is also seen in *Amia* ("*Paramiatus*") *gurleyi* Romer and Fryxell (1928). *A. gurleyi* is less distinct than its describers believed, and while relatively shorter than *A. calva*, appears "deep-bodied" primarily as a result of the shorter body and of crushing. Its opercular series is very similar to that of *A. fragosa* and it has similar frontal-parietal proportions.

As noted above, *Amia russelli* Janot (1966) from the late Paleocene of France is also close to this group in several characters. The parietal Janot figures (*ibid.*, pl. IX, fig. 5) is about as wide as long, contrasting with that of *A. calva* (cf. e.g. Janot, 1967, pl. IV, fig. 6) and resembling that of *A. kehreri*, *A. munieri*, *A. gurleyi*, and *A. fragosa*. The frontal figured for *A. russelli* (Janot, pl. IX, fig. 3) is about 2.8 times as long as the figured parietal, and the latter is of about the proper size to fit the frontal. Orbital excavation in the frontal is also similar to that of *A. fragosa*. Frontal-parietal proportions of *A. russelli* thus seem to have been similar to the three species noted above. Operculum shape of *A. russelli* is generally similar to that of Cretaceous and Eocene species, being taller than wide, although the posterior angle is slightly below the middle of the bone, as in *A. calva*.

The relatively narrow proportions of the opercular series of the fossil species is a primitive character for amiids. In *A. calva* the series has widened as a result of general body elongation, although the operculum itself is always wider than or as wide as high regardless of size of the animal (Fig. 3, *c-e*).

It is thus clear that the late Cretaceous and Paleocene species discussed above are closely related, and the similarities indicate that little evidence exists for maintaining separate species *A. fragosa*, *A. russelli*, *A. gurleyi*, and *A. kehreri*. The oldest available name for the species discussed here is *A. kehreri* Andreae (1892).

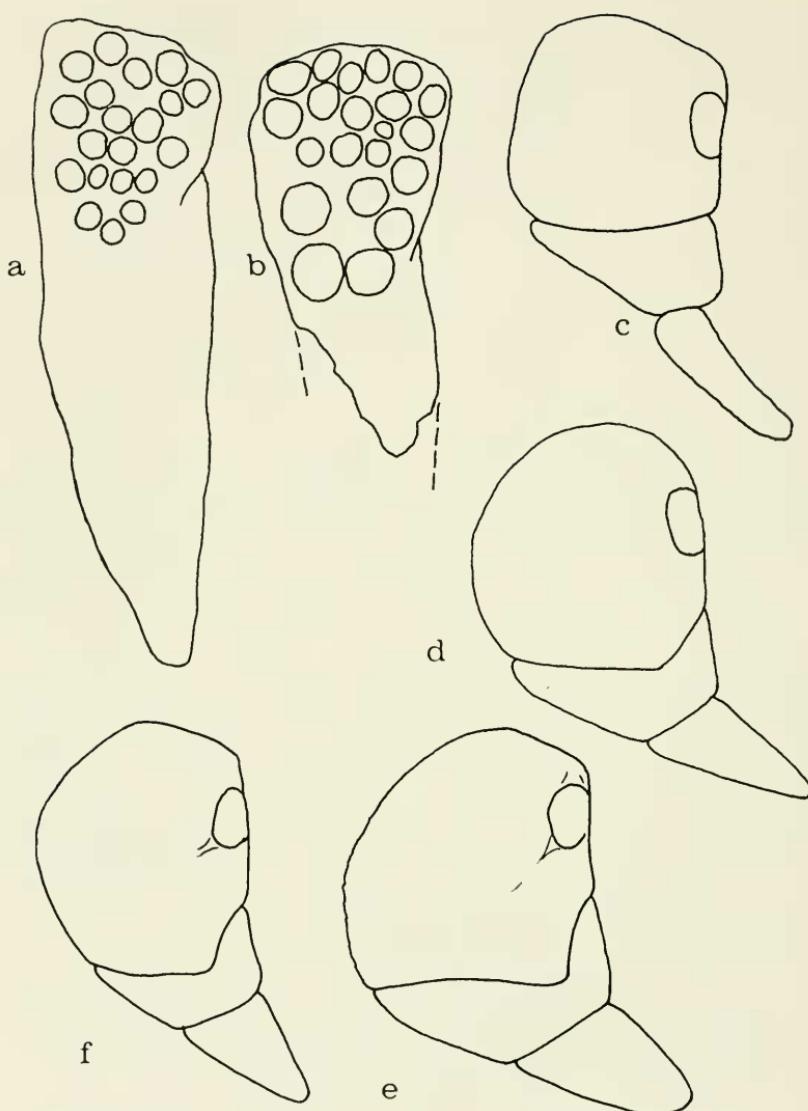


Fig. 3. *a*, *Amia calva*, ventral view of left vomer. *b*, *A. fragosa*, the same, Hell Creek Formation, Montana, MCZ 9287. *c-e*, *A. calva*, medial views of left opercular series; sizes: *c*, MCZ 8970, Standard Length 45 mm, *d*, MCZ 35780, SL 155 mm, *e*, unnumbered MCZ specimen, SL 425 mm. *f*, *A. fragosa*, restoration of opercular series. Note that in *c-e* operculum is wider than tall, whereas in *f*, Figure 4, and Plate I, it is taller than wide. *a-b*,  $\times 3$ ; *e-f*,  $\times 1$ ; *c-d* not to scale.

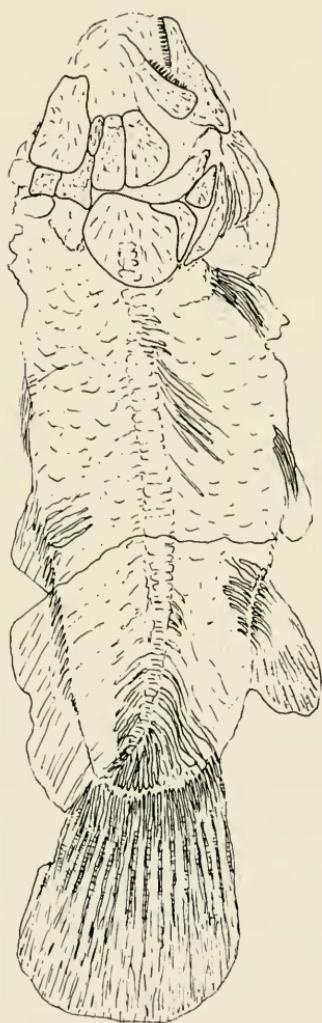


Fig. 4. *Amia kehreri*, middle Eocene, Messel bei Darmstadt. Sketch of BM (NH) P33480 made from a photograph taken by the senior author.  $\times$  about  $\frac{1}{2}$ .

We believe that *A. kehreri* and *A. fragosa* may be synonymous; temporal and geographic separation are the only known differentiating characteristics. The type of *A. kehreri* is from Messel, as are the British Museum (Natural History) specimens of this species noted above. The type is a partial skeleton, but shows the expanded lower postorbital (Andreae, 1895, pl. 1, fig. 15) more clearly seen in BMNH P33480 (Fig. 4) and the Geiseltal specimens (Pl. 1). *A. gurleyi* (Romer and Fryxell, 1928, fig. 1) also resembles *A. kehreri* in close approximation of dorsal and caudal fins, and this may be an indication that synonymy of *A. gurleyi* with *A. kehreri* is in order. Since both are middle Eocene, only geographic separation and a few minor details suggest that two species be maintained. Presence of the supraorbital canal in the parietal, somewhat larger size, and a few other superficial features seem to distinguish *A. russelli*. We do not formally synonymize any species here, however, until other early and middle Cenozoic European specimens can be studied; our purpose is merely to point out the close similarity of these Cretaceous and early Cenozoic forms (see also Estes, Hecht, and Hofstetter, 1967).

There is thus a closely related group of species of *Amia* (some probably synonymous) that is known from Cretaceous through middle Eocene of North America, and late Paleocene to at least early Oligocene of Europe. This group of species is distinct from *A. calva* only in superficial and essentially primitive ways, including relatively shorter body and skull and minor proportional differences of skull roof and mandibular bones.

The morphology of *A. fragosa* and the close relationship of North American Cretaceous seas to the Mississippi River drainage (Estes, 1964) indicate that *A. fragosa* itself cannot be far from the ancestry of the Recent bowfin. Further studies of European amiid remains, of articulated specimens of "Protamia" at Princeton University (Estes, 1964, p. 42), and of growth series of *A. calva* will be of considerable interest in tracing the ancestry of the modern species (see also Simpson, 1937, p. 59; specimens lost).

*Stratigraphic range of Amia fragosa.* Regardless of possible synonymy with European species, as noted above, the stratigraphic range of *A. fragosa* is remarkably long, extending from late Cretaceous through at least middle Eocene time in North America. No criteria exist at present for naming more than the one species. The major deposits in which remains of *A. fragosa* have been found are summarized in Table I. Unpublished records are taken from collections at the American Museum of Natural History, Princeton University, and the United States National Museum.

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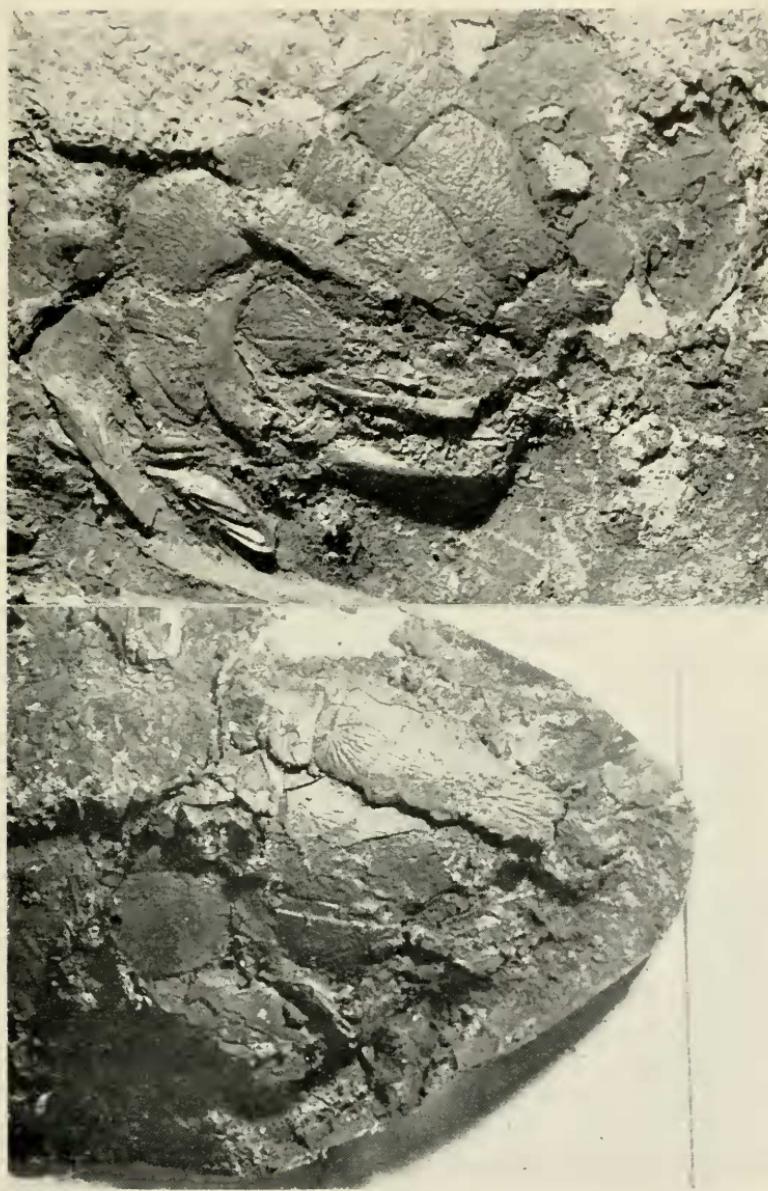


Plate I. *Amia kehreri*, middle Eocene, Geiseltal deposits. Above, skull of one individual in lateral view, showing expanded lower postorbital, opercular series, and frontal-parietal proportions; below, skull of another individual in dorsal view showing frontal-parietal proportions;  $\times$  about 1.

			WYOMING	MONTANA	S. DAKOTA	CANADA
CENOZOIC	EOCENE	L				
		M	Bridger Fm., Green River Fm., Wasatch Fm.			Golden Valley Fm.
		E				
PALEOCENE		L		Melville beds		
		M	Rock Bench beds	Fort Union Fm.	Tongue River member	Paskapoo Fm.
		E	Mantua lentil		Tullock member	
CRETACEOUS	MAESTRICHIAN		Lance Fm.	Hell Creek Fm.		Edmonton Fm.
	CAMPANIAN		"Mesaverde" Fm.	Judith River Fm.		Oldman Fm.

Table I. Major deposits carrying remains of *Amia fragosa* in the Western Interior of the United States and Canada. Nomenclature of units varies with author; we have therefore deliberately chosen a conservative terminology.